

MYCORRHIZAL FUNGI AND THE INTEGRATION
OF PLANT AND SOIL NUTRIENT DYNAMICS

KEY WORDS: Mycorrhizal fungi, plant nutrition, microorganisms

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ABSTRACT

Mycorrhizal fungi have been studied in relation to plant uptake or fungal concentration of C, N, P, Ca, Mg, S, Na, Mn, B, Cu, Zn, Si, Br, Cl, I, Pb, Co, Ni, Fe, and Cd. Of these, the direct or indirect acquisition of P and N by plants has been intensively researched. Mycorrhizal fungi are known to influence plant photosynthesis, transpiration, physiology including hormone levels and source-sink relationships, plant biomass and root exudation. Mycorrhizal fungi can also affect plant water uptake, soil structure and soil microbial populations. The direct interaction of mycorrhizal fungi with soil organic matter and transformations of nutrients by soil microorganisms needs further study. Knowledge of these areas is essential to fully integrate our understanding of soil nutrient availability, plant nutrient uptake and utilization, and the fate of organic or mineral nutrients applied to the soil.

INTRODUCTION

The involvement of mycorrhizal fungi in plant growth and nutrition is among the most exciting and challenging areas of agricultural research today: It is exciting because of the number of directions from which one can approach it; and it is challenging because of its potential for maximizing fertilizer use efficiency. In this paper we will present an overview of the effects of mycorrhizal fungi on plant nutrition. Our primary objective is to integrate the many facets of this field, as well

as present some recent developments. Much of the information is available in review articles to which the reader will be directed. We will draw almost entirely upon literature dealing with Vesicular-Arbuscular Mycorrhizal (VAM) fungi because of our own interests and the dominance of VAM host plants in the plant kingdom. For a thorough background on all types of mycorrhizal fungi and their interaction with plants, the reader should consult the work of Harley and Smith (1), and the Proceedings of the Sixth North American Conference on Mycorrhizae edited by R. Molina (2).

MORPHOLOGY OF VA MYCORRHIZAE

Mycorrhizae are grouped into various categories according to the plant host and fungus involved, and certain morphological features (1). VAM fungi form arbuscules, but not always vesicles, within roots. Arbuscules are dichotomously branched haustoria which invaginate the plasmalemma of root cortical cells without disrupting or destroying the cells (3). These organs function in the exchange of C and P (and possibly other nutrients) between the plant and fungus. Vesicles are globose structures which occur within or between cortical cells and serve as nutrient reservoirs for the fungus.

An extensive, interconnecting network of fungal mycelium integrates the internal root environment with the surrounding soil. The mycelium of these fungi can colonize and bridge the root systems of the same or different plant species (4,5). In addition to the uptake of water and nutrients, hyphae produce various types of resting spores which are used for species identification.

MINERAL UPTAKE BY MYCORRHIZAE

Hyphae in the soil are able to take up mineral nutrients and transport them to the host plant where they become incorporated into plant tissues (6). Mycorrhizal fungi have their most significant effect on improving plant growth when elements such as P, Zn, or Cu are limiting (1,7-9). The enhanced uptake of heavy metals (Cd, Zn, Cu, Ni, Pb, Fe, and Co) by mycorrhizal plants may be detrimental to plant growth (10) although there is some indication that VAM fungi may increase the plant's tolerance to these metals (11). Toxic accumulations of Br have been found in mycorrhizal plants grown in fumigated soil (12), but phytotoxic concentrations of I were found to be inconsistent (13). Chloride and the concentrations of other major anions (SO_4 , H_2PO_4 and NO_3) occur at higher levels in VAM than non-VAM plants¹⁴. Both VAM and P-amended plants had lower total cation (K, Ca, Mg and Na) concentrations but P addition did not duplicate the VAM fungal effect on anions. From this study it was concluded that

VAM and P-amended, non-VAM plants reduced their cation excess by different mechanisms.

The role of VAM fungi in plant P nutrition and the effects of P fertilization on mycorrhizae are reviewed elsewhere (1,15,16). Briefly, fungal hyphae can take up P from the soil solution, concentrate it into polyphosphates within the hyphae, and release P to the plant via the arbuscules. This becomes important when plant-available P is very low in the soil. P-amended, non-VAM controls are frequently used to determine if enhanced plant P uptake caused by the mycorrhizal fungus is the reason for increased growth and the higher levels of other nutrients observed in VAM plants. For some elements such as Zn and Cu, the fungus may function similar to P fertilization (17); however, this does not appear to be the case with Cl, Br, K or Fe (13,17).

Current information suggests that VAM and non-VAM plants obtain P from the same pools in the soil but that VAM fungi are able to exploit available P sources which are inaccessible to roots (16). It is also possible that there is an interaction between hyphae and soil microorganisms in the mineralization and uptake of organic or soluble, inorganic P sources (16).

The role of VAM fungi in plant N uptake can be by direct or indirect means (18). Hyphae can acquire ^{15}N from organic and inorganic sources placed several centimeters from the nearest root, and make it available to the plant (19). In another ^{15}N study, VAM plants were able to take up more N from the non-labelled pool than the controls (20). VAM and non-VAM plants may draw differentially upon N sources in the soil.

Nitrogen-fixation in mycorrhizal and non-mycorrhizal legumes has been reviewed recently (21,22). Although there is a general belief that P-fertilization can duplicate the effects of the VAM fungus on symbiotic N_2 -fixation, new reports are suggesting that non-P-mediated influences by VAM fungi on the legume-Rhizobium-VAM symbiosis can occur (23-25).

Two additional reports involving mycorrhizal legumes and plant nutrition should be mentioned. In one study, VAM plants grown in a soil low in B responded better to B application than non-VAM plants (26). The addition of NH_4NO_3 to enhance B deficiency eliminated the beneficial effect of the VAM fungus. This may have resulted from a negative effect of NH_4NO_3 on the functioning of Rhizobium and the VAM fungus.

Another report described the significant increase of Si in soybean resulting from mycorrhiza formation but not P fertilization (27). It was suggested that the plant Si content may be related to the activity of the VAM fungus.

PLANT PHYSIOLOGY, PHOTOSYNTHESIS AND WATER RELATIONS

The complexity of the mycorrhizal association becomes evident when one examines how the plant responds to mycorrhiza formation (1,16,28). Mycorrhizal plants have higher chlorophyll concentrations (29) and photosynthetic rates (30) than non-VAM plants. Carbon source-sink relationships (16,31), reduced stomatal resistance (32), and altered hormone content (33,34) of mycorrhizal plants may contribute to the observed effects on photosynthesis. These factors may also increase the drought tolerance of VAM plants over that of non-VAM plants (32,35). Recent studies found that mycorrhizal legumes utilized soil water against steeper water potential gradients than non-VAM plants (36,37). This suggests that mycorrhiza formation in plants will lower their permanent wilting potential; however, this result may vary with soil texture (38,39).

SOIL STRUCTURE AND MICROBIOLOGY

The soil environment not only influences the effect VAM fungi have on plant growth, but evidence is also accumulating that these fungi favorably affect soil structure. We found that the formation of water-stable soil aggregates, total soil porosity, and soil water permeability were improved with mycorrhizal plants compared with non-mycorrhizal controls (40). Experiments currently in progress are attempting to separate the direct effects of VAM fungal hyphae on soil structure from indirect effects attributable to enhanced growth of the mycorrhizal root system.

Research conducted under field conditions is needed to better understand the impact VAM fungi have on soil structure and plant nutrition (41). Such studies are difficult because of the complex interactions of soil microorganisms in substrate decomposition and nutrient cycling (42,43). However, plant and soil ecologists are now considering VAM fungi as important components in soil nutrient cycling processes (42,44). The concept of a mycorrhizosphere is gaining acceptance as a useful tool in understanding the nutrient and microbial dynamics near mycorrhizal root systems. The mycorrhizosphere is the zone of soil which contains mycorrhizal plant roots and where nutrient availability and soil microbial populations differ quantitatively and qualitatively from that of non-mycorrhizal plants (45-48). Experiments with VAM fungi which have shown hyphal connections between plants, and the transfer of P and N from one plant to another, serve to emphasize the importance of the mycorrhizosphere in plant nutrition (4,5,49,50).

Although root exudation may be altered when plants become mycorrhizal (51), it is unclear how microbial populations along the root surface will respond to these changes (52). Recent approaches to the study of microbial-mycorrhiza interactions have

included the assessment of functional microbial groups which share certain nutritional or physiological traits (48,53). This method of study may be very useful in providing information on the availability or utilization of specific nutrients in the mycorrhizosphere.

Most of our discussion has been directed towards nutrient uptake by the fungus and subsequent response by the plant. We will now address the much neglected area of carbon input to the soil via VAM fungal mycelium and how this may indirectly affect plant nutrition. Since VAM fungi acquire most of their carbon from the host plant, any enhancement of plant growth by the fungus also stimulates hyphal growth in the soil. The extraradical hyphae and spores which consist of chitin, lipids, fats, and other concentrated nutrients, provide an energy rich substrate for the soil microbiota (47,54). Parasitism or grazing on VAM hyphae could release substrates which stimulate microbial activity, and this may affect plant nutrient availability. The proliferation of VAM hyphae at sites rich in organic matter (55), and the potential utilization of VAM hyphae by the resident microflora as a source of C, N or P, may stimulate decomposition of organic materials. It would be worthwhile to examine plant nutrient uptake from the decomposition of sterilized VAM and non-VAM roots. It may very well be that VAM roots decompose faster, thus providing a more rapid turnover of nutrients than non-VAM roots. This type of an experiment may also explain why plant growth responses are occasionally observed in plants inoculated with pot culture material (VAM spores, mycorrhizal roots, hyphae and soil) even though very low levels of infection occur.

One of the drawbacks of studying extraradical mycelium is the difficulty in its quantification. A soil chitin assay has been used to quantify VAM fungal biomass, but the presence of clay or organic matter may adversely affect the results (56). Other methods, used with some success, have estimated the length of VAM fungal hyphae (19,57). Significant correlations have been found with hyphal length determinations and ^{15}N uptake by celery (19), and between hyphal length and the formation of water-stable soil aggregates (40). Therefore, some methods are available to study extraradical mycelium, but more work in this area is needed. Unfortunately, none of the methods cited above can differentiate between living and dead hyphae. This information would be of significant help in studying the growth and survival of extraradical hyphae.

Studies now in progress by us are revealing new insights into interactions between extraradical mycelium and soil organisms. We are finding a close association between chitin-decomposing actinomycetes and VAM fungal spores and hyphae. Many of these actinomycetes are able to bind soil together into water-stable aggregates. This suggests that VAM hyphae are providing a physical framework and nutrient stimulus for actinomycetes and

other microflora in the improvement of soil structure and stability.

CONCLUDING REMARKS

This paper brings together some new and some well-known information on VAM fungi and plant nutrition. The emphasis on microbial interactions is an attempt to stimulate more research in this area. The soil microflora, including VAM fungi, and microfauna have long been recognized for their contributions to plant growth and nutrition (58,59), yet new threads of information are continually being pulled from this complex fabric. It is our belief that the growth of VAM fungi within and exterior to roots; their ability to physically link roots of the same or different plant species; their proliferation in soil organic matter; their impact on soil structure; their interactions with soil microorganisms; their uptake and transport of nutrients to and from the plant; and the response of the plant to these activities, all provide evidence that VAM fungi truly integrate their host plants with the soil environment.

REFERENCES

1. Harley, J. L. and S. E. Smith. 1983. "Mycorrhizal Symbiosis". Academic Press, London.
2. Molina, R. (ed.). 1985. "Proc. Sixth North American Conference on Mycorrhizae". Forest Research Lab. Oregon State Univ., Corvallis.
3. Bonfante-Fasolo, P. 1984. pp. 5. In "VA Mycorrhiza". C. L. Powell and D. J. Bagyaraj, (eds.). CRC Press, Boca Raton, Florida.
4. Heap, A. J. and E. I. Newman. 1980. New Phytol. 85:169.
5. van Kessel, C., P. W. Singleton and H. J. Hoben. 1985. Plant Physiol. 79:562.
6. Rhodes, L. H. and J. W. Gerdemann. 1980. pp. 173. In "Cellular Interactions in Symbiosis and Parasitism". C. B. Cook, P. W. Pappas and E. D. Rudolph (eds.). Ohio State Univ. Press, Columbus.
7. La Rue, J. H., W. D. McClellan and W. L. Peacock. 1975. Calif. Agric. 29(5):6.
8. Lambert, D. H. 1982. Can. J. For. Res. 12:1024.

9. Gildon, A. and P. B. Tinker. 1983. *New Phytol.* 95:263.
10. Killham, K. and M. K. Firestone. 1983. *Plant Soil* 72:39.
11. Gildon, A. and P. B. Tinker. 1983. *New Phytol.* 95:247.
12. Jakobsen, I. 1983. *New Phytol.* 94:595.
13. Buwalda, J. G., D. P. Stribley and P. B. Tinker. 1983. *New Phytol.* 93:217.
14. Buwalda, J. G., D. P. Stribley and P. B. Tinker. 1983. *Plant Soil* 71:463.
15. Woolhouse, H. W. 1975. pp. 209. In "Endomycorrhizas". F. E. Sanders, B. Mosse and P. B. Tinker (eds.). Academic Press, London.
16. Cooper, K. M. 1984. pp. 155. In "VA Mycorrhiza". C. L. Powell and D. J. Bagyaraj (eds.). CRC Press, Boca Raton, Florida.
17. Lambert, D. H., D. E. Baker and H. Cole. 1979. *Soil Sci. Soc. Am. J.* 43:976.
18. Bowen, G. D. and S. E. Smith. 1981. In "Terrestrial Nitrogen Cycles: Processes, Ecosystem Strategies and Management Impacts". F. E. Clark and T. Rosswall (eds.) Swedish Natural Science Research Council, Stockholm. *Ecol. Bull.* 33:237.
19. Ames, R. N., C. P. P. Reid, L. K. Porter and C. Cambardella. 1983. *New Phytol.* 95:381.
20. Ames, R. N., L. K. Porter, T. V. St. John and C. P. P. Reid. 1984. *New Phytol.* 97:269.
21. Barea, J. M. and C. Azcon-Aguilar. 1983. *Adv. Agron.* 36:1.
22. Munns, D. N. and B. Mosse. 1980. pp. 115. In "Advances in Legume Science". R. J. Summerfield and A. H. Bunting (eds.). Royal Botanic Gardens, Kew. *Proc. Int. Legume Conf.*, Kew.
23. Rajapakse, S. and J. C. Miller, Jr. 1986. *Plant Soil*, in press.
24. Pacovsky, R. S., G. J. Bethlenfalvay and E. A. Paul. 1986. *Crop Sci.* 26:151.
25. Ames, R. N. and G. J. Bethlenfalvay. 1986. *New Phytol.* in press.

26. Lambert, D. H., H. Cole and D. E. Baker. 1980. *Plant Soil* 57:431. 45.
27. Yost, R. S. and R. L. Fox. 1982. *Agron. J.* 74:475. 46.
28. Moser, M. and K. Haselwandter. 1983. pp. 391. In "Physiological Plant Ecology III. Responses to the Chemical and Biological Environment". O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (eds.). Springer-Verlag, Berlin. 47.
29. Allen, M. F., J. C. Sexton, T. S. Moore, Jr. and M. Christensen. 1981. *New Phytol.* 87:687. 48.
30. Johnson, C. R. 1984. *Plant Soil* 80:35. 49.
31. Bayne, H. G., M. S. Brown and G. J. Bethlenfalvay. 1984. *Physiol. Plant.* 62:576. 50.
32. Allen, M. F., W. K. Smith, T. S. Moore, Jr. and M. Christensen. 1981. *New Phytol.* 88:683. 51.
33. Allen, M. F., T. S. Moore, Jr. and M. Christensen. 1980. *Can. J. Bot.* 58:371. 52.
34. Allen, M. F., T. S. Moore, Jr. and M. Christensen. 1982. *Can. J. Bot.* 60:468. 53.
35. Allen, M. F. and M. G. Boosalis. 1983. *New Phytol.* 93:67. 54.
36. Bethlenfalvay, G. J., M. S. Brown, R. N. Ames and R. S. Thomas. 1986. *Plant Physiol.* in press. 55.
37. Hardie, K. and L. Leyton. 1981. *New Phytol.* 89:599. 56.
38. Dakessian, S., M. S. Brown and G. J. Bethlenfalvay. 1986. *Plant Soil* 94:439. 57.
39. Bethlenfalvay, G. J., J. M. Ulrich and M. S. Brown. 1985. *Soil Sci. Soc. Am. J.* 49:1164. 58.
40. Thomas, R. S., S. Dakessian, R. N. Ames, M. S. Brown and G. J. Bethlenfalvay. 1986. *Soil Sci. Soc. Am. J.* in press. 59.
41. Fitter, A. H. 1985. *New Phytol.* 99:257. 59.
42. Coleman, D. C., C. P. P. Reid and C. V. Cole. 1983. pp. 1. In "Advances in Ecological Research", Vol. 13. A. Macfadyen and E. D. Ford (eds.). Academic Press, New York. 59.
43. Clarholm, M. 1985. *Soil Biol. Biochem.* 17:181.
44. Chapin, F. S. III. 1980. *Ann. Rev. Ecol. Syst.* 11:233.

45. Linderman, R. G. 1985. pp. 117. In "Proc. 6th North American Conference on Mycorrhizae". R. Molina (ed.). Forest Research Lab, Oregon State Univ. Corvallis.
46. Meyer, J. R. 1985. pp. 121. In "Proc. 6th North American Conference on Mycorrhizae". R. Molina, (ed.). Forest Research Lab, Oregon State Univ., Corvallis.
47. Bagyaraj, D. J. 1984. pp. 131. In "VA Mycorrhiza". C. L. Powell and D. J. Bagyaraj (eds.). CRC Press, Boca Raton, Florida.
48. Ames, R. N., K. L. Mihara and G. J. Bethlenfalvay. 1986. Biol Fert. Soil, in press.
49. Heap, A. J. and E. I. Newman. 1980. New Phytol. 85:173.
50. Whittingham, J. and D. J. Read. 1982. New Phytol. 90:277.
51. Graham, J. H., R. T. Leonard and J. A. Menge. 1981. Plant Physiol. 68:548.
52. Ames, R. N., C. P. P. Reid and E. R. Ingham. 1984. New Phytol. 96:555.
53. Meyer, J. R. and R. G. Linderman. 1986. Soil Biol. Biochem. 18:191.
54. Moore, J. C., T. V. St. John and D. C. Coleman. 1985. Ecology 66:1979.
55. St. John, T. V., D. C. Coleman and C. P. P. Reid. 1983. Ecology 64:957.
56. Pacovsky, R. S. and G. J. Bethlenfalvay. 1982. Plant Soil 68:143
57. Abbott, L. K., A. D. Robson and G. De Boer. 1984. New Phytol. 97:437.
58. Dommergues, Y. R. and S. V. Krupa (eds.). 1978. "Interactions Between Non-pathogenic Soil Microorganisms and Plants". Elsevier Scientific Pub. Co., Amsterdam.
59. Todd, R. L. and J. E. Giddens (eds.). 1984. "Microbial-Plant Interactions". Amer. Soc. Agron. Special Publication 47. Soil Sci. Soc. Am., Am. Soc. Agron. and Crop Sci. Soc. Am., Madison.